

"Marine Mammal Commission Workshop on Future Directions in Marine Mammal Research."

"Determining Units to Conserve"

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I. Goals/Objectives

Two human generations ago, my great-grandparents paused in their westward move while herds of migrating buffalo crossed the Missouri River in front of their steamboat. Long before the birth of my father the migratory herds of the North American great plains were a distant memory and the plains ecosystems were forever changed. The marine world is different. Fencing or paving the sea is impossible. Nevertheless, the great migrating "herds" of whales were nearly extinguished in my lifetime. Humans now choose what they will conserve into the future. The question of how to define "units to conserve" is not a question of how to define a species, but rather how we define our vision of the future.

Conservation science provides the knowledge needed to implement the vision. A cruise up the inland waterways of southeastern Alaska would today provide views of humpback whales, killer whales, harbor porpoise, harbor seals, Steller sea lions and sea otters. A vision of maintaining a healthy ecosystem complete with these top predators may involve using science to understand how these populations are structured. This structure can be from the species level (how many species of killer whales occupy these waters) to the much smaller scale of population units that experience little interaction with neighboring populations from year to year.

In the terrestrial world in the United States, management of natural resources has been so poor that the primary conservation law has the objective of not letting species go extinct. Fortunately, marine systems are today in better condition allowing the opportunity to envision healthy connected marine ecosystems. Although most marine mammal populations are now recovering from past over-exploitation, some are in serious decline and most are likely to face increased risks as human populations continue to increase. Interpreting the risks posed by specific human activities must be done in light of how the animal populations structure themselves, how the animals' habitats are likely to change and what society envisions for the future. There are already two laws that embody that vision with respect to marine mammals: the Marine Mammal Protection Act and the Endangered Species Act. Although the Acts are extremely important for conservation, both have a somewhat blurry vision when it comes to actually implementing the laws.

Much of the difficulty is not so much in the vision of the laws but derives from the mismatch of the human propensity to categorize and the seamless continuity of nature. The complexity of nature does not fit simply into categories like "species", "sub-species",

“distinct population segments” or “population stocks”. The purpose of this manuscript is to provide an understanding of conservation unit concepts by reviewing these concepts in the laws and by considering how these concepts pertain to marine mammals in particular. A series of case studies on killer whales, Steller sea lions and harbor seals will be used to illustrate UTC concepts and problems. I chose these cases as a minimum set to illustrate what I feel are the research and management needs regarding UTCs: adequate treatment of uncertainty in taxonomy; incorporating the precautionary principle and shifting the burden of proof, development and testing of tools to define stocks in a probabilistic manner, and development of the definition of stocks by managers that incorporates scientific uncertainty in a precautionary manner. I then conclude with research and management needs to begin to improve our understanding of marine mammal population structure and hence appropriate UTCs for different management objectives.

II. Units of Conservation in U.S. law:

A. The Endangered Species Act

The ESA defines species (Section 3(15)) as “any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature.” Regarding Distinct Population Segments (DPSs) Congress (Senate Report 151, 96th Congress, 1st Session) instructed the Secretary of the Interior to exercise this authority “...sparingly and only when the biological evidence indicates that such action is warranted.” Prior to a Joint Agreement on the definition of DPSs, the idea of defining populations as evolutionarily significant units to preserve the genetic diversity of the species was applied to Pacific salmon (Waples 1991). Dizon et al. (1991) offer a phylogeographic approach that categorizes stocks as to their probability of being an evolutionarily significant unit, a unit used under the Endangered Species Act. Many of these ideas were captured in a Joint Agreement to define by regulation the term “distinct population segment.”

1. Summary of the Joint Agreement

The Fish and Wildlife Service and the National Marine Fisheries Service, jointly charged with implementing the Act, agreed to definition DPSs in the “Policy Regarding the Recognition of Distinct Vertebrate Population Segments” (USFWS 1996). Under the policy, three elements are to be considered sequentially in determining the status of a potentially distinct population segment: 1) the discreteness of the population relative to the rest of the species; 2) the significance of the population segment to the species; and 3) the population segment’s conservation status in relation to the Act’s standards for listing (i.e., is the population segment endangered or threatened when treated as if it were a species?). Further criteria are given for each element.

Element I- Discreteness

A population segment of a vertebrate species may be considered discrete if it satisfies one of the following criteria: 1) It is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. 2) It

is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(1)(1)(D) of the Act.

Element II-Significance

If a population segment satisfies at least one of the above criteria for discreteness, its biological and ecological significance will then be considered. This consideration may include, but is not limited to the following: 1) Persistence of the discrete population segment in an ecological setting unusual or unique for the taxon. 2) Evidence that the loss of the discrete population segment would result in a significant gap in the range of the taxon. 3) Evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant as an introduced population outside its historic range. 4) Evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics. Because precise circumstances are likely to vary considerably from case-to-case, it is not possible to describe prospectively all the classes of information that might bear on the biological and ecological importance of a discrete population segment.

Element III-Status

If a population segment is discrete and significant (i.e., it is a distinct population segment), its evaluation for endangered or threatened status will be based on the Act's definition of those terms and a review of the factors enumerated in section 4(1). It may be appropriate to assign different classifications to different distinct population segments of the same vertebrate taxon.

2. Status of DPSs under the ESA for already listed marine mammal species

To be completed with a table of the listed species and DPSs.

3. Illustrative recent cases of DPS definition for marine mammals

a. Southern Resident killer whales

In 2001, the National Marine Fisheries Service (NMFS) was petitioned to list Southern Resident killer whales (*Orcinus orca*) as threatened or endangered under the Endangered Species Act (ESA) and to designate critical habitat for these whales. After concluding that an ESA listing may be warranted, NMFS formed a Biological Review Team (BRT), comprised of scientists with diverse backgrounds, to conduct a status review.

The BRT determined that Southern Residents meet the criterion for “discreteness” under the joint NMFS/U.S. Fish and Wildlife Service (USFWS) ESA policy based on genetics and other information. However, the determination of “significance” was far more difficult, largely because of issues surrounding killer whale taxonomy. Because the BRT was unable to achieve consensus, a vote was taken that resulted in the agency decision not to list these killer whales. The process exposed a number of critical issues relating to the concept of unit to conserve and all of these issues involved the treatment of uncertainty.

In the face of uncertainty, the field of taxonomics is not precautionary. Correctly identifying the killer whale taxon proved critical, because the criteria used to evaluate “significance” of a DPS are defined relative to other populations within that taxon. Formal taxonomic changes are often slow to occur and lag behind current knowledge. In the case of killer whales, the typical requirements of a good sample size of adult skulls could result in taxonomic inaction for decades because skulls can only now be obtained through the slow accumulation of skulls from stranded animals. If there are pelagic forms of killer whales (which is likely) skulls may never be attainable. Nevertheless, the BRT concluded that there are sufficient data to conclude that the current designation of one global species for killer whales is likely inaccurate. The types of data that are likely to be available in a more timely manner are genetic data, morphological data that do not require dead animals like photographs of coloration patterns and simple metrics like dorsal fin shape and perhaps lengths from some areas where aerial photogrammetry is possible. There is a need for taxonomists to confront the problems of how to make taxonomic designations in the face of uncertainty. To date, the burden of proof has fallen on scientists to have overwhelming evidence of taxonomic separation, including skulls, before a new species or sub-species is accepted by the scientific community. For DPSs to be designated on a proper management timeframe, a new process needs to be developed to designate provisional taxonomic units using the best available data but not restricted to requiring all data prior to designation. In particular, further work is needed to better interpret the “significance” of genetic differences across taxa.

Interpretation of “significant portion of the range” is clouded by shifting baseline issues: uncertainty about what the range of the taxon has been in the recent past. Even if the taxonomic issues above had been resolved and the “Resident” or “fish eating type” of killer whale was considered the appropriate taxon, there remained issues of defining the range of Residents. These uncertainties fell into two main categories: the knowable and the unknowable. The knowable uncertainties concerned defining the current range of Resident killer whales, which are currently known to exist between Puget Sound and the Alaska Peninsula. It is suspected that the Resident form may be found further to the west perhaps ranging to Russia and Japan where there are also salmon runs, thought to be a primary prey. Also, the winter range of Residents, including Southern Residents, remains unknown. These knowledge gaps can be filled by more extensive genetic biopsy sampling and through satellite tagging of known Residents.

It is more difficult, if not impossible, to fill knowledge gaps about historical distribution. It is known that Southern Residents and their prey have both declined in the past few decades. Thus, it is plausible that range contraction has already occurred. Although the primary range of SRs currently known is Puget Sound/San Juan Islands, they could have occupied waters that formerly sustained much larger salmon runs (in terms of biomass), such as waters off Oregon and California. Although it may be possible to reconstruct historical range through genetic examination of teeth from museums, it may also occur that no data are available and the problem of historical range becomes “unknowable”. In this case, “significant portion of the range” can be based on either current range or inferred range where inference is drawn from defining suitable habitat. The problem of “shifting baselines”, where the pristine or baseline condition is defined as the state of the

population when it was first studied, is pronounced for marine populations where historical distributional data are scarce. It is particularly problematic for species like killer whales, where presence/absence-type data cannot be used because different potential sub-species (like the fish-eating “residents” and the mammal-eating “transients”) are cryptic.

The final DPS “significance criterion” relates to evidence that the Southern Residents differ markedly from other populations in genetic characteristics. Speciation is a complex process that does not lend itself to simple categorization. Killer whales are a particularly illustrative example of the problem of reducing biological complexity to simple categories for use in a legal framework. Apparently, there is a selective advantage for killer whales to become dietary specialists and adapt their social organization accordingly. Within the North Pacific there are at least three types of killer whales that are genetically distinct. Residents are fish-eaters that specialize in salmon and form relatively large pods (10-20 individuals) that are strictly matrilineal. Both males and females nearly always remain within the pod of their birth. Most mating occurs with individuals from other pods. Transients are mammal-eaters that are found in much smaller groups. It is unlikely that these groups are strictly matrilineal because it is common to see one or two males alone for long periods. Little is known of the third type, Offshores, except that they have a large group size and some have been observed eating fish. Since these types are sympatric and nevertheless appear genetically isolated, they meet the definition of a biological species.

Nuclear and mitochondrial DNA data are consistent with no current gene flow between these types and the magnitude of differences are quite large (larger than for many acknowledged species). However, interpretation of significance remains difficult. The low genetic diversity together with both low population size and a social organization that would result in an even lower effective population size suggest that genetic drift is likely to be large. This means that genetically large differences can accrue relatively rapidly. Further, it is possible that metapopulation dynamics could make founder events likely. In this case, local populations become extinct and are recolonized on a frequent basis. When small populations are founded from a larger population a phenomenon called “lineage sorting” can occur. Imagine that there is a large population that has lived in an ocean basin for many thousands of generations. This population would contain many haplotypes, which can be thought of as family names. Some names will be old and some new and these names may differ by many letters. If new populations are created from the large old population, there is the possibility that the new populations will contain different frequencies of the names. If these new populations are small and drift such that they end up with only a single name (lineage) then interpretation of the relation of these new populations to one another can be incorrect without understanding the history. For example, if one population ended up with an “old” name and its neighbor ended up with a “new” name, then one could incorrectly infer that they had been separated for a time long enough to develop all the letter changes (mutations) between the names. The correct relationship (that they have been recently founded from a large population) can only be reached by considering lineage sorting.

For a behaviorally complex animal, like killer whales, there is likely to be considerable uncertainty in interpreting genetic data. Acknowledging this uncertainty results in admitting that there will never be a genetic litmus test for determining when genetic data indicate a “marked” difference. Instead, a checklist of the type of genetic differences that contribute to evolutionary significance together with guidelines on how to treat uncertainty would prove more beneficial. For example, if fewer than one disperser per generation is consistent with the ability of populations to maintain local adaptations then a guideline for “markedly” like “a 10% chance that there are fewer than ten dispersers per generation” would allow the incorporation of uncertainty, including factors like lineage sorting. Of course, putting genetic results in a probabilistic context will require a case-specific modeling approach.

b. Steller sea lions

In the initial listing of Steller sea lions, the species was divided into two Distinct Population Segments (Loughlin et al. 1997) using criteria in Dizon et al. (1991). Although the sample size was small and the distributional coverage had significant gaps, the genetic differences between the eastern and western strata were so large that taken together with the strong differences in trends between the regions, evidence was considered sufficient to designate two DPSs. There are two interesting considerations in this listing that relate to the idea of UTCs: the precedent of drawing a boundary in an area with no genetic data, and the non-consideration of an additional UTC for which there were genetic differences but no strong trend differences.

In the designation of the eastern and western DPSs, there were no genetic data from Prince William Sound, which was between the nearest known areas of genetic differences: the Kodiak archipelago and Lowerie Islands in Southeast Alaska. However, Prince William Sound better matched the Kodiak Archipelago with respect to trend (a negative trend compared with the positive trends in Southeast Alaska) and habitat (adjacent to the Gulf of Alaska). However, it is interesting that the agency was willing to move forward in setting a boundary without corroborative genetic data.

In contrast, the same genetic study that underpinned the DPS definition (Bickham et al. 1996) also showed significant genetic differences between the Asian populations and the nearest populations in the Aleutian Islands. This paper did not emphasize these frequency differences because the differences were not as large as those found between the eastern and western strata. However, it could be argued that the genetic data were sufficient to consider the Asian populations discrete at which point the three criteria for “evolutionary significance” would be considered: significant portion of the range, unique habitat and marked genetic differences. There is no record that the Asian population was considered for DPS status despite there being a good likelihood that the Okhotsk Sea populations may be considered to constitute “evolutionary significance” for either the unique habitat or the significant portion of the range criteria.

Thus, it appears that the agency was precautionary in the instance of setting apart an area with an obvious increasing trend but not precautionary with an equivalent amount of data

when trend differences were not apparent. The example highlights the need for consistent use of a checklist and a consistent policy on treating uncertainty for DPS definition.

B. Marine Mammal Protection Act (MMPA): managing to preserve population stocks as functioning elements of the ecosystem

1. Review of terminology

The word “stock” is a management term defined in the context of a particular management regime in this case by law in the Marine Mammal Protection Act (MMPA). The Act specifies that endangered or depleted species "and populations stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part, and consistent with this major objective, they should not be permitted to diminish below their optimum sustainable population...". The Act further states that "the primary objective of their management should be to maintain the health and stability of the marine ecosystem. Whenever consistent with this primary objective, it should be the goal to obtain an optimum and sustainable population keeping in mind the carrying capacity of the habitat." As guidance to interpreting these management objectives, the Act defines "optimum sustainable population" (OSP) as: "with respect to any population stock, the number of animals which will result in the maximum productivity of the population or the species, keeping in mind the carrying capacity of the habitat and the health of the ecosystem of which they form a constituent element." By regulation, the National Marine Fisheries Service defined populations to be at OSP when they were between carrying capacity and the maximum net productivity level (MNPL) (Gerrodette and DeMaster 1990). Furthermore, the Act defines "population stock" as "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature."

In a paper aimed at giving better quantitative guidance to implement these goals, Taylor (1997) developed a functional definition for population stock for use in calculating the number of animals that can be removed from populations and that is consistent with both the population and ecosystem management goals of the Act. I repeat the development of that functional definition here as it is used in several of the case-studies below. The 1994 Amendments to the Act allow regulation of human-caused mortality through the calculation of Potential Biological Removals (PBRs). One element of the equation used to calculate PBR is an estimate of abundance. Presumably, this estimate is made for each population stock. Use of the term “population stock” implies that both a biological (population) and a management (stock) meaning were intended. For brevity, I use "stock" instead of "population stock" and it carries the same double meaning: (1) groups that are delineated by a very low rate of genetic exchange, or (2) groups of animals that are essentially demographically separate. Such groups will experience differential risk and therefore should be managed separately. A group of animals is considered “demographically separate” when the rate of animals coming into that population from its neighbors is so low that if this population were to decline it

would not be rescued by its neighbors over a period of decades. These two meanings are often referred to by separate names, the strongly genetically differentiated group being called an evolutionarily significant unit (equivalent to a DPS) and the demographically separate group, a management unit. Moritz (1994) regards stocks to be synonymous with management units and argues that they are the logical unit for short-term management. Perrin and Brownell (1994) contend that "stock" identity cannot be divorced from the management strategy adopted. There is no doubt that population units that are significant in an evolutionary sense qualify as population stocks under the MMPA. However, preserving only evolutionarily significant units could allow reduction and/or fragmentation of present ranges and thus violate the ecosystem goals of the MMPA.

As an example, consider the schematic distributions in Figure 1. Distribution "a" is the pristine distribution where width represents abundance and length represents geographic distance. Constrictions in this schematic represent limited movement such that this distribution could be described as a series of populations connected by dispersal (the aggregate is often called a metapopulation). If we reduced abundance by 50%, we could obtain any of the other distributions: b, range contraction; c, range fragmentation; or d, range maintenance. Although all may meet the population goal of maintaining harbor seals within OSP, i.e., about 0.5K, b and c likely do not meet the ecosystem goal. However, because there are no population definition "rules" for calculating PBRs, any of these alternatives could occur depending on the distribution of human-caused mortality.

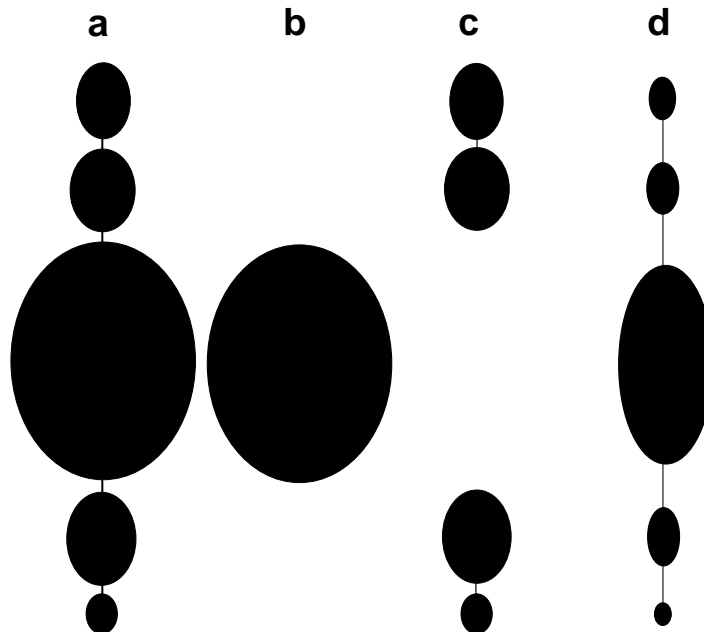


Figure 1. Distribution of pristine populations (a), versus potential distributions after 50% of the total abundance is removed. Width represents abundance, length represents distance.

The Act's definition of population stock gives little guidance. Unfortunately, for most species, managers have found it impossible to use the criterion "interbreed when

mature." If we interpret "interbreed when mature" to represent the degree of genetic interchange, then nature presents us with a continuum. Some geographically separate groups of animals may exchange members at the rate of one per generation and others at the rate of one percent per year. If we restrict our definition of population stock to only those virtually closed populations exchanging individuals at the rate of only a few individuals per generation then we will only have population boundaries encircling large geographic ranges. These ranges may be composed of disparate habitats. Calculating the PBR based on abundance estimates for these units may allow depletion of areas with large human-caused mortalities, i.e., result in distributions b and c.

Irrespective of difficulties defining populations, the National Marine Fisheries Service must nevertheless draw lines on a map to represent population boundaries, and they must do it for the 48 marine mammal species that occur in U.S. waters. Available data for making such population boundary decisions ranges from very crude distributional data to very detailed data on movement, morphology, genetics and distribution. Most of the time, however, to meet the Act's management objectives, the implementing agency must make adequate decisions in the face of considerable uncertainty.

There are two types of errors that can be made in making these decisions: (1) incorrect lumping of populations, which could result in not reaching MNPL or even eliminating one population, or (2) incorrect splitting, which may unnecessarily restrict human activities. Call the first the "under-protection error," and the second the "over-protection error." To calculate the probabilities of making these errors, management objectives must be defined quantitatively. For purposes of illustration, we assume that population growth is logistic and thus MNPL occurs at 50% of carrying capacity (K). If maintenance of populations above 50% of K were the only objective, any of the distributions in Figure 1 would be an acceptable management outcome. However, because the Act emphasizes ecosystem integrity, a more comprehensive management target is required, i.e., one that considers range. Only Figure 1d would be an acceptable outcome if management objectives are to both maintain populations above MNPL and maintain an unfragmented and undiminished range.

Participants in a workshop to provide guidelines for implementing the MMPA recognized that maintaining the range would serve to meet the ecosystem goals (Wade and Angliss, 1997). The stock definition section of this report states:

Many types of information can be used to identify stocks of a species: distribution and movements, population trends, morphological differences, genetic differences, contaminants and natural isotope loads, parasite differences, and oceanographic habitat differences. Evidence of morphological or genetic differences in animals from different geographic regions indicates that these populations are reproductively isolated. Reproductive isolation is proof of demographic isolation, and thus separate management is appropriate when such differences are found. Failure to detect differences experimentally, however, does not mean the opposite. Dispersal rates, though sufficiently high to homogenize

morphological or genetic differences detectable experimentally between putative populations, may still be insufficient to deliver enough recruits from an unexploited population (source) to an adjacent exploited population (sink) so that the latter remains a functioning element of its ecosystem. Insufficient dispersal between populations where one bears the brunt of exploitation coupled with their inappropriate pooling for management could easily result in failure to meet MMPA objectives. For example, it is common to have human-caused mortality restricted to a portion of a species' range. Such concentrated mortality (if of a large magnitude) could lead to population fragmentation, a reduction in range, or even the loss of undetected populations, and would only be mitigated by high immigration rates from adjacent areas.

Therefore, careful consideration needs to be given to how stocks are defined. In particular, where mortality is greater than a PBR calculated from the abundance just within the oceanographic region where the human-caused mortality occurs, serious consideration should be given to defining an appropriate management unit in this region. In the absence of adequate information on stock structure and fisheries mortality, a species' range within an ocean should be divided into stocks that represent defensible management units. Examples of such management units include distinct oceanographic regions, semi-isolated habitat areas, and areas of higher density of the species that are separated by relatively lower density areas. Such areas have often been found to represent true biological stocks where sufficient information is available. There is no intent to define stocks that are clearly too small to represent demographically isolated biological populations, but it is noted that for some species genetic and other biological information has confirmed the likely existence of stocks of relatively small spatial scale, such as within Puget Sound, WA, the Gulf of Maine, or Cook Inlet, AK.

2. Review of SAR definitions of stocks (number of stocks/species, justification, average stock area)

To be completed with a simple table of the number of stocks for different species by Regions.

3. Examination of revealing cases

a. Harbor seals

Harbor seals do not have obvious gaps in their distribution that allow easy stock definition. Definition of stocks has differed by region (Alaska, the contiguous US west coast and the east coast), which provides alternate views on definition of units to conserve. The degree of attention paid to stock definition has been commensurate with risks, with the many areas of decline warranting extensive studies within Alaska and the

remaining areas of increasing populations depending on academic studies not driven by MMPA stock definition needs.

The decline of harbor seals over much of their Alaskan range remains a conservation concern because the cause is unknown and the animals are the subject of a subsistence harvest. Harbor seals are an important subsistence resource for many Alaska Native coastal communities, with an estimated annual take of 2,200-2,800 seals (Wolf, 2001; Alaska Native Harbor Seal Commission (ANHSC), 2001). Management objectives are thus concerned not only with maintaining harbor seals as functioning elements of their ecosystem but also meeting agreed co-management goals to ensure that this species remains a sustainable resource (MMPA as amended 1994; NMFS-ANHSC, 1999).

The National Marine Fisheries Service (NMFS) currently recognizes three separate stocks of harbor seals in Alaska, identified primarily on the basis of regional differences in trend (Small and DeMaster, 1995; Hill et al., 1997; Angliss et al. 2001). At the time of their designation, however, it was recognized that large gaps existed in our knowledge of dispersal and movement patterns and population structure, and it was recommended that more information on these aspects of seal biology were required to define more meaningful management units (Small and DeMaster, 1995; DeMaster 1996). Over the past decade, a large body of research has been conducted that greatly improves our understanding of harbor seal population structure including further trend studies and directed studies on movement patterns and population genetic structure (summarized in O'Corry Crowe et al. 2003).

Analyses of genetic data revealed a minimum of 12 demographically distinct stocks. These stocks were consistent with tagging data that revealed low levels of movement and with trend data that revealed, for example, three different trends even within Southeast Alaska (where three stocks were proposed based on genetic data that were consistent with the trend data). However, even with this useful increase in data relating to population structure, significant gaps remain in the sampling distribution such that data cannot be used to suggest stock definition in those areas. A specific example is the area between Glacier Bay and the Copper River Delta. Although Glacier Bay has apparently experienced a strong decline in the past decade and there are local concerns about the status of seals in Yakutat together with a subsistence harvest, there are still insufficient samples upon which to base scientific advice. Thus, despite improvement, management still faces the problem of how to define stocks in the face of uncertainty. This is particularly problematic in light of continuing declines in areas where there are subsistence hunts. It remains to be seen how the co-management agreement will perform in such a case where timely decisions are needed for already depleted populations, such as those found in Prince William Sound.

In contrast, trends in abundance are increasing or stable on both coasts of the contiguous US. There are x stocks defined from Puget Sound south to the California/Mexico border. A primary source of data to define these stocks was a genetic study (ref). This study made no attempt to sample evenly this geographic range, but rather compared samples from y quite distant locations and found all to significantly differ. This is similar to a

study on the Alaskan harbor seals that concluded that the seals conformed to an isolation-by-distance model (Westlake & O'Corry Crowe 2002). However, the latter study noted that this scale was likely too large for conclusions concerning stock structure to be drawn. Martien and Taylor (in press) showed that the use of hypothesis testing to draw conclusions about stock structure for populations that were continuously distributed and isolated-by-distance resulted in defining too few populations. They showed that the strongest statistical evidence for population structure (statistical power) was obtained by dividing the range in half, even if the true structure contained many populations. This resulted from two factors: 1) comparing only two strata directly compared the individuals that differed the most from opposite ends of the range (statistically speaking this comparison has the largest effect size), and 2) each strata has the largest possible sample size with further sub-division resulting in fewer samples in each strata (statistically speaking the comparison with the greater sample size has higher precision). An important conclusion was that although statistical significance reveals that there is population structure present, it provides *no evidence* for the placement of the boundary between stocks. Thus, the correct interpretation of the hypothesis testing done in Ref (19xx) is that there are at least x stocks in the area examined, but no conclusions can be drawn about stock boundaries in the area.

East coast description

The amount of attention paid to gathering further data regarding stock definition relates to the degree of risk that stocks face when definition is improper. In the cases where trends are stable or increasing and there are no areas of concentrated human kills, no management errors can be made even if stock definition is wrong. The Alaskan situation differs both because some areas are declining or have declined significantly in the recent past and because there are areas of concentrated human impact. Further, there is a co-management agreement that strives to maintain sustainable local hunting. Poor stock definition could easily result in failure to meet both MMPA and co-management objectives.

The scientific challenge with respect to defining stocks is to both gather data that allow stock definition and to develop analytical methods that minimize errors in stock definition. A new method, called Boundary Rank (Martien and Taylor, in review) was created and performance tested specifically to avoid the errors known to plague other genetic analytical methods. Most methods require scientists to stratify their data prior to analysis, which can strongly influence results particularly for continuously distributed species like harbor seals. Further, no other analytical methods have been performance tested for use in defining management units (demographically independent populations). Another important research need is better methods to integrate disparate types of data in a rigorous fashion. For example, data on distribution, trends in abundance, contaminant levels, morphology, timing of migration or reproductive events, acoustics, telemetry, and genetics all contribute to understanding population structure but relate to that structure on different scales (both spatial and temporal). Although it is not likely that a single analytical method can be developed to integrate these data, it would be helpful to at least

have a review available to guide when and some methods concerning how these data can be used to strengthen stock definitions.

The management challenge is to decide how to treat uncertainty in stock definition both when there are sufficient data and when data are either poor or entirely lacking. In cases where there are data but the data indicate potential non-trivial levels of dispersal, management guidance is needed to transition from uncertain data to decisions regarding stock definition. A form of words that would promote transparent definition in the face of uncertainty would be; “a geographic group of animals will be considered a stock if internal recruitment plus dispersal from neighboring populations has a 90% probability of maintaining the local population at greater than 50%K.” An alternative “rule of thumb” definition that would not consider such detailed population dynamics as the previous definition would be “a stock is a population for which the best estimate for the dispersal rate with a neighbor is less than 1/2%/year, where 1/2%/year is considered to be demographically trivial”.

There is a need to improve stock definition when data are insufficient for making such probabilistic statements. Elements that would allow good definition in the face of this high degree of uncertainty should: 1) use all available data on scale of population structure from areas with sufficient data, 2) provide incentive to gather the requisite data, 3) be precautionary in step with the degree of risk engendered by not making correct stock definition decisions.

b. Steller sea lions

Although the western DPS of Steller sea lions is listing under the ESA and receives the strongest protection under that Act, identifying the cause of the decline and making recommendations for recovery are likely to be impacted by definitions of UTCs on a smaller scale. Steller sea lions have been considered to be a metapopulation (York), i.e. a set of interconnected populations whose total behavior can only be understood by knowing the interconnections between the smaller parts or units. Metapopulations are often characterized by source/sink dynamics, where a source is defined by positive population growth and a sink by negative growth. The strength of the connections between the different units (i.e. the level of dispersal) can determine whether the sinks dominate and completely drain the metapopulation to extinction or whether the sources predominate and allow the metapopulation to remain extant despite the frequent loss of many of its constituent parts. This is clearly a concern for understanding the risk facing the western DPS because there are some rookeries that are still rapidly declining, some that are apparently stable and some that are increasing.

In such situations, with some areas of strong decline, it is better in the near term for the metapopulation to have low connectivity. With extremely low levels of dispersal, areas of positive growth can maintain that growth while neighboring areas continue to decline. Thus, although some of the healthy stock is leaking out through the drain of dispersal, there is more than enough internal recruitment to maintain positive growth. In times of peril it is better to have low connectivity/dispersal. In contrast, in times of recovery it is

better to have high connectivity/dispersal so that healthy populations can assist/rescue misfortunate neighbors. Irregardless, the full risk to the DPS cannot be understood without knowledge concerning UTCs that are akin to stocks under the MMPA.

Another important feature of understanding UTCs at the stock level is that this is the level needed to interpret trends in abundance, which in turn are needed to fathom the causes of decline. Consider a situation where rookeries in the western portion of the DPS are in strong decline while those in the east are either stable or increasing. Knowing that these areas are demographically independent will improve prioritization decisions on both research and conservation actions.

Currently there are only two stocks defined for Steller sea lions that are the same as the DPSs. Although calculation of PBRs, which are used to suggest which commercial fisheries should reduce direct mortality, is likely to be ineffective, defining demographically independent stocks is still important to management under both Acts. The primary reason why definition of stocks is important is to assist in identifying causes for the decline and total risk to the DPS. However, even though Steller sea lions are currently in the ESA emergency room, the objective is to recover to a point where the MMPA, which strives to maintain Steller sea lions as functioning elements of their ecosystem, is the relevant management law. Scientists should be attempting to gather information on what makes for a healthy Steller sea lion population while the mandate of the ESA provides scientists the wherewithal to generate the data.

C. Conclusions

Research and management needs regarding UTCs are: adequate treatment of uncertainty in **taxonomy**: incorporating the precautionary principle and shifting the burden of proof, **development and testing of tools** to define stocks in a probabilistic manner, and **development of the definition of stocks by managers** that incorporates scientific uncertainty in a precautionary manner.

1. Taxonomy

The field of taxonomy has been an academic pursuit. Traditionally, the scientific process is conservative with a large burden of proof placed on the scientist to prevent false acceptance of hypotheses. With conservation decisions awaiting taxonomic progress, this process becomes dysfunctional because avoidance of potentially false hypotheses gives undue preference to avoiding false taxonomic definitions without regard to conservation consequences. A number of actions would reduce conservation problems relating to taxonomic issues: 1) development and prioritization of a list of taxonomic uncertainties for marine mammals, 2) agreement on a method to provisionally list taxonomic entities pending attainment of data, 3) systematic filling of data gaps by priority in point 1, 4) agreement by taxonomists on a list of factors to consider in defining species and sub-species using genetic data together with other life history traits, agreement by morphologists and molecular biologists on necessary and sufficient conditions for

provisional taxonomic listing, and 5) a statement of definition that explicitly incorporates the treatment of uncertainty.

2. Analytical tool testing and development

Although some analytical tools developed to address evolutionary questions have been “tested” for a limited number of factors (often a single case study), only one method has been tested for performance at defining management units. Performance testing uses data originating from simulations where the truth is known to evaluate how different methods perform in a specific management context. This testing is needed for data interpretation for both managers and researchers.

Ideally, research should be analyzed so that results can be directly used in conservation decisions. More methods designed specifically for such applied problems are needed. Another need for analytical development is tools that allow researchers to better design studies of population structure. For example, researchers should be able to say how many samples and how many genetic markers will be needed to provide a given level of certainty about dispersal rates. Scientists interested in detecting trends in abundance have such tools that allow them to either estimate prior to a study their ability to detect a given trend with a certain power after a number of surveys. However, in part because the definition of UTC remains nebulous, researchers are unable to state how many samples/markers they will need or to state after a study the probability that if several units were within their study area whether they would have detected them given their sample size and distribution.

Methods have been suggested that allow full presentation of the uncertainty in the data without a specific definition of UTC. For example, Taylor suggested the use of error trade-off curves (Taylor and Dizon 1996). Trade-off curves have the important advantage of not forcing the researcher into making the decision of what error ratio is appropriate for management. Consider, for example, Figure 2. Taylor and Dizon (1999) argue that in matters of population structure, policy must precede science because the data can only be properly interpreted once the policy decision has been made concerning what level of population structure is being sought. Although this is true, use of error trade-off curves at least allows scientists to present results without the need to choose an error ratio. However, as seen in Figure 2, either some choice has to be made on what dispersal rate is appropriate or scientists must present a range of possibly relevant dispersal rates, which becomes computationally burdensome.

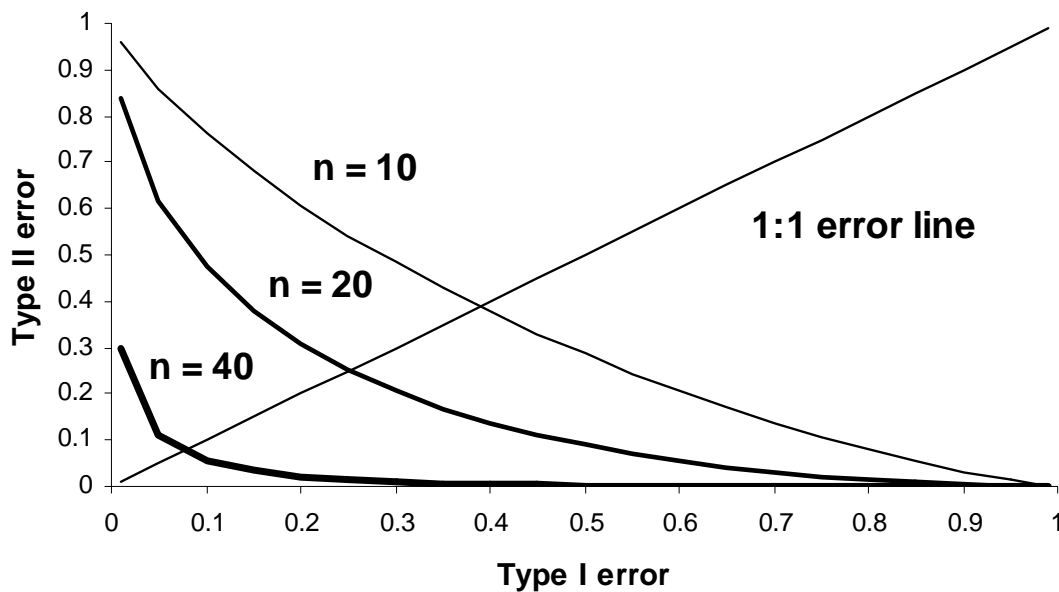


Figure 2. Error trade-off curves for a null hypothesis of panmixia between two populations and an alternate hypothesis of a dispersal rate of 0.75%/year between two populations. The alternate hypothesis is true. Using the typical significance criterion of a Type I error (α) of 0.05, the Type II error would be 0.85, 0.60, and 0.10 for sample sizes (n) of 10, 20 and 40 respectively. Using this criteria means that the scientist is promoting Type II/Type I error ratios of 17 (0.85/0.05), 12 (0.60/0.05), and 2 (0.10/0.05) for the different sample sizes. In other words, when $n = 10$ the scientist by using $\alpha = 0.05$ is 17 times more willing to incorrectly lump populations than to incorrectly lump populations. Another alternate decision framework is deciding to equalize the Type I and Type II errors, which is shown in the 1:1 error line. Using this decision process would result in using $\alpha = 0.40$ (rather than $\alpha = 0.05$) when $n = 10$.

3 Incorporating scientific uncertainty into management definitions of stock

The discussion in point 2 clarifies the rationale for better definition of the meaning of stock by managers, but does not suggest how such definitions can incorporate uncertainty. The development of the PBR scheme incorporated the idea of incorporating uncertainty to proscribe precautionary management (Taylor et al. 2000, Taylor & Wade 2002). Incorporation of uncertainty was accomplished through use of quantitative criteria like “a 90% chance of a population being greater than 50% of historical numbers in 100 years.” These definitions all have a statement of probability linked to a desired state in a given time period. The statement of probability results in situations with less certainty receiving more conservative management because such management is needed to ensure reaching the desired management state.

An equivalent statement that incorporates uncertainty would be beneficial for stock definition. An example of such a statement would be “a geographic group of animals will be considered a stock if internal recruitment plus dispersal from neighboring

populations has a 90% probability of maintaining the local population at greater than 50%K.”

Figure 3 symbolizes linked populations with water bottles linked by unknown levels of flow between the bottles. In 3A understanding the linkage between the bottles is not necessary because water flow out from the system is equal across the “range” of the bottles. In contrast, 3B has strong flow from only a single “location” in the bottle “range”. If the objective is to keep all bottles at a level of at least 50% then not only must the “structure” be known (how many bottles and how much water is in each bottle) but the level of flow is critical if you know that the bottle experiencing heavy outflow cannot sustain the flow without input from neighbors.

For populations of animals that are continuously distributed, there is uncertainty about the level of human caused mortality, the number of demographically independent units, the location of “boundaries” and the amount of dispersal between units. The scientific challenge should be to quantify all those uncertainties. The management/policy challenge is to phrase policy in a fashion that allows the best use of our knowledge while acknowledging the impact of our ignorance.

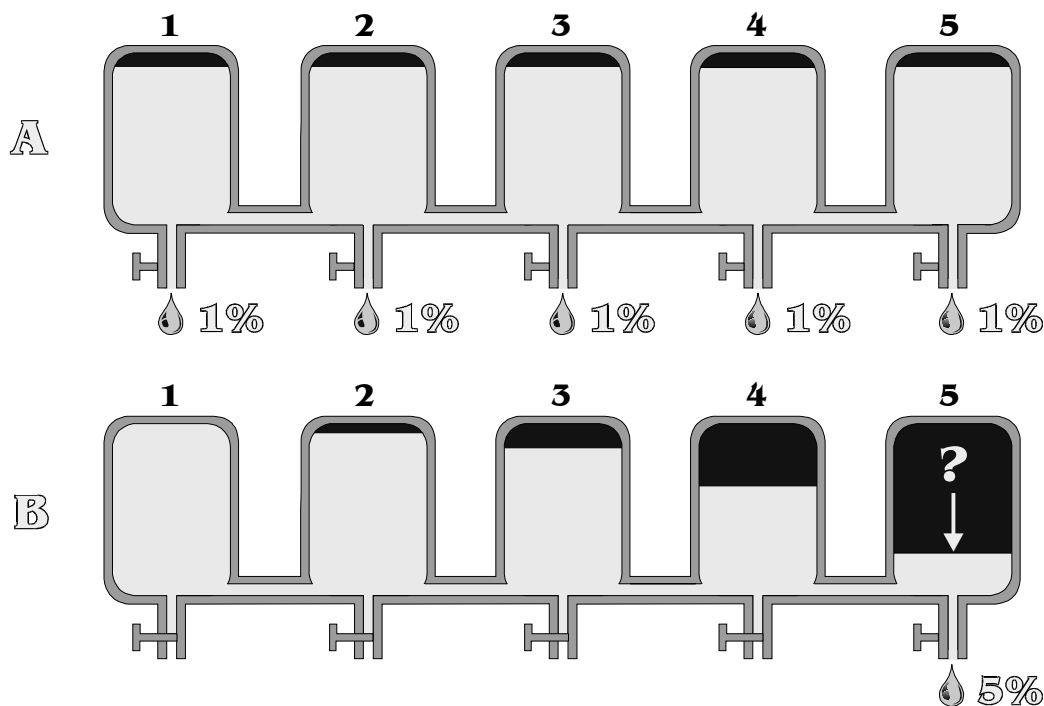


Figure 3. Population structure depicted as a connected system of water bottles with removals from the system shown as drains.

Prioritizing needs for stock definition: is inconsistent treatment “bad”

A review of the Stock Assessment Reports suggests that stock definition is not consistent either within species or across Regions. This is exemplified by harbor seals where Alaska may soon have over a dozen stocks while the remaining west coast has 3 and the east coast has only one. However, such inconsistent definitions do not necessarily mean

that management will be inconsistent. For example, if populations are more or less evenly growing and healthy along the west coast and no areas have large kills, then regardless of how stocks were defined, none would warrant a “strategic” or “depleted” listing and therefore no management is required (the equivalent of Figure 3A).

A rough idea of how stock definition research could be prioritized would be to arbitrarily partition a species’ range into units based on the smallest known or likely scale. If areas reveal the potential of strategic status then further research is warranted. Further prioritization could be based on the ratio of known kill to estimated PBR based on the worst-case stock scenario.

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